Vocal production mechanisms in the budgerigar (*Melopsittacus undulatus*): The presence and implications of amplitude modulation

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In this paper acoustic evidence is presented for the presence of amplitude modulation in budgerigar (*Melopsittacus undulatus*) contact calls and learned English vocalizations. Previously, acoustic analyses of budgerigar vocalizations have consisted solely of visual inspection of spectrograms or power spectra (derived from Fourier transformation). Such analyses have led researchers to conclude that budgerigar vocalizations are primarily frequency-modulated, harmonic vocalizations. Although budgerigar calls have been shown to contain regions that are modulated in amplitude, the implications of this fact have been largely ignored. Amplitude modulation, the nonlinear interaction between two separate signals that results in the creation of new, heterodyne (sum and difference) frequencies, can produce a very complex Fourier spectrum that may resemble that produced by a harmonic vocalization. In this paper, the acoustic principles necessary for identifying amplitude modulation present in signals are outlined, and followed by data demonstrating that amplitude modulation is a prominent feature not only of natural budgerigar contact calls, but also of their learned English vocalizations. It is illustrated how analyzing a vocalization that contains amplitude modulation as if it were harmonic can result in misinterpretations of the acoustic and physical properties of the sound and sound source. The implications of amplitude modulation for studies of the ontogenetic, physical, and neural basis of budgerigar vocalizations are discussed, and a potential model for how the budgerigar syrinx may function to produce amplitude modulation is proposed. © *1999 Acoustical Society of America.* [S0001-4966(99)03607-3]

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INTRODUCTION

A. Budgerigar vocal mechanisms

Natural budgerigar (parakeet) vocalizations, including contact calls and some warble song elements, have been described and investigated as frequency-modulated, harmonic signals (Heaton *et al.*, 1995; Brittan-Powell *et al.*, 1997a,b). Studies have examined the ontogeny of spectrally represented frequency modulations in calls (Brittan-Powell *et al.*, 1997a; Hall *et al.*, 1997), the effects of syringeal denervation on spectral characteristics of calls (Heaton *et al.*, 1995; Shea *et al.*, 1997), and whether production in helium alters spectral features of calls produced by syringeal denervated and normal budgerigars (Brittan-Powell *et al.*, 1997b). Acoustic features of budgerigar vocalizations have been compared to those of Gray parrots (*Psittacus erithacus*, Turney *et al.*, 1994), and humans (Silaeva, 1998). These studies, however, analyzed only the frequency spectra derived via Fourier techniques, specifically, frequency by time ''spectrograms'' or amplitude by frequency ''power spectra.''

Budgerigar contact calls, however, also display significant modulation in amplitude (Dooling and Searcy, 1981, 1985). A call may contain several frequency changes, but amplitude fluctuations are ubiquitous and easily identified in displays of both the gross temporal envelope and amplitude

waveform [Fig. 1(A) and (B), respectively; amplitude by time representations of the signal]. As demonstrated here, some of this amplitude fluctuation is due to nonlinear amplitude modulation. When amplitude modulation is present in a signal, its Fourier spectrum contains additional frequency components that are produced not by the primary source(s), but rather by nonlinear interactions between two originally independent signals (Nowicki and Capranica, 1986a, b; Bradbury and Vehrencamp, 1998). To date, no study of budgerigar calls or warble song has explained the complex array of observed spectral components, investigated whether the observed spectral components are generated by a mechanism of amplitude modulation, nor examined how amplitude modulation develops ontogenetically, is produced, or is affected by perturbations of the vocal production system (e.g., neural or mechanical). Given the spectral complexity of vocalizations that can be produced by amplitude modulation, perturbations affecting that modulation may be difficult or impossible to detect in a cursory inspection of a Fourier spectrum (either spectrograms or power spectra). Indeed, cursory analyses of vaguely harmonic-like signals have led to inaccurate interpretations of the acoustic, physical, and neural mechanisms underlying avian vocalizations that contain amplitude modulation [e.g., in chickadees (Greenewalt, 1968), and in budgerigars (Heaton *et al.*, 1995 and Brauth *et al.*, 1997)].

The fact that budgerigars produce amplitude-modulated signals is itself significant. Budgerigars have a syrinx with one set of opposable membranes [like all parrots, but unlike

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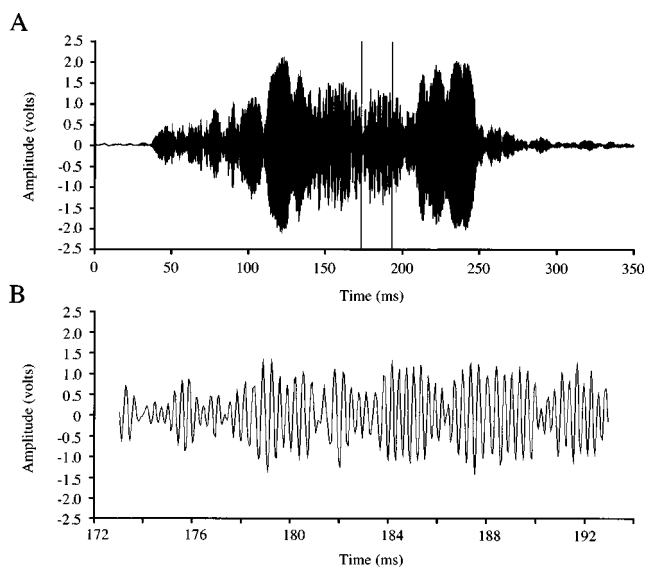
FIG. 1. A budgerigar's contact call (Forest). (A) The entire amplitude envelope. (B) Amplitude waveform of a 20-ms expanded time window from the call in (A) (173–193 ms) showing aperiodic fluctuations of the amplitude. Note the extensive modulation of amplitude that occurs throughout the call.

passerine birds that have a bipartite syrinx with two sets of membranes (Evans, 1969; Nottebohm, 1976; Gaunt and Gaunt, 1985; Suthers, 1997)], and only two pair of intrinsic syringeal muscles (Evans, 1969; Gaunt and Gaunt, 1985). Moreover, parrots are thought not to have independent control of their syringeal membranes (Nottebohm, 1976; Heaton *et al.*, 1995; Brittan-Powell *et al.*, 1997b; Brauth *et al.*, 1997). Learning how budgerigars produce two independent source signals that interact nonlinearly to produce amplitude modulation will further our understanding of syringeal mechanisms that underlie complex avian vocal productions.

In this paper, I show that budgerigars produce amplitude modulation both in their natural contact calls and when mimicking human vowel sounds. First, I redescribe key acoustic and spectral features that allow identification of a sound produced by amplitude modulation, and how nonlinear interactions generate new frequencies. I use the term ''redescribe'' intentionally, because I review material from two overlooked papers by Nowicki and Capranica (1986a, b) on the existence and implications of amplitude modulation in avian vocalizations. Moreover, because a thorough understanding of acoustic principles is necessary to evaluate the vocalizations I present, I also describe two other signal types that must be distinguished from amplitude-modulated ones in the analysis of any vocalizations: Vocalizations known as harmonic, and those produced from a linear interaction (or beating) between harmonic signals.

B. Acoustic characteristics of signals containing harmonics, amplitude modulation, and beating

The relationship between the amplitude waveform and its Fourier spectrum is critical for understanding the physical nature of any sound. The amplitude waveform is the true representation of a signal in the time domain, and is free of mathematical transformation. The wave shape of the ampli-

tude waveform displays how frequency, amplitude, and phase of a signal vary with time. A Fourier transformation, by definition, transforms the signal into the frequency domain. A Fourier analysis decomposes each user-specified time window of an amplitude waveform into a series of pure sinusoids that, when added, produce the observed waveform. For any signal, conclusions based on independent analyses of time and frequency domains must concur. I thus describe the relationship between time and frequency domains for signals that contain harmonics, amplitude modulation, and beating.

1. Harmonics

A harmonic signal is one in which the amplitude waveform repeats itself exactly (i.e., is periodic). A pure tone or sinusoid (a signal composed of only one frequency) is the simplest form of harmonic sound, and is represented in a Fourier spectrum (i.e., either a spectrogram or a power spectrum) by a single component at the frequency the waveform repeats; this frequency is known as the fundamental frequency.

More complex, nonsinusoidal harmonic waveforms (signals composed of multiple frequencies, termed multifrequency harmonic signals) are represented in a Fourier spectrum by an array of evenly spaced energy components (also known as a harmonic ''stack'' in a spectrogram). The fundamental frequency of the vocalization (known as the first harmonic) is usually the lowest frequency component; successive frequency components are located at exact-integer multiples of the fundamental. A multi-frequency harmonic vocalization with a waveform that repeats every 5 ms thus has a fundamental frequency of 200 Hz and component frequencies at 200, 400, 600 Hz, $n \times 200$ Hz, the fundamental may also be calculated as the highest common denominator of the component frequencies. A sound is classified as ''harmonic'' because, and only because, it repeats exactly in the time domain. Perfectly harmonic biological signals (i.e., where repetition is exact from one period to the next), however, are rare, and some fluctuation usually exists in their periodicity. This fluctuation, or ''quasi-periodicity'' (Titze, 1994), can cause higher harmonics in natural signals to be at near rather than exact-integer multiples of the fundamental frequency (e.g., if a fundamental frequency is 200 ± 2 Hz, the first several harmonics would be at close multiples of 200, but the 10th harmonic could be located at 2000 ± 20 Hz).

Figure 2(A) shows the amplitude waveform of a representative multi-frequency harmonic signal with a fundamental frequency of 183 Hz, and Fig. 3(A) is a schematic of the power spectrum (a representation of the signal after Fourier transformation) that would be generated by this signal. The waveform repeats identically every 5.5 ms, and the harmonics of the fundamental frequency are at 366, 549, and 732 Hz in the power spectrum.

2. Amplitude modulation

An amplitude-modulated vocalization is produced when one signal, the carrier signal, is modulated in amplitude by a second, the modulating signal. In general, the carrier signal has the greater frequency, and is modulated by the lower
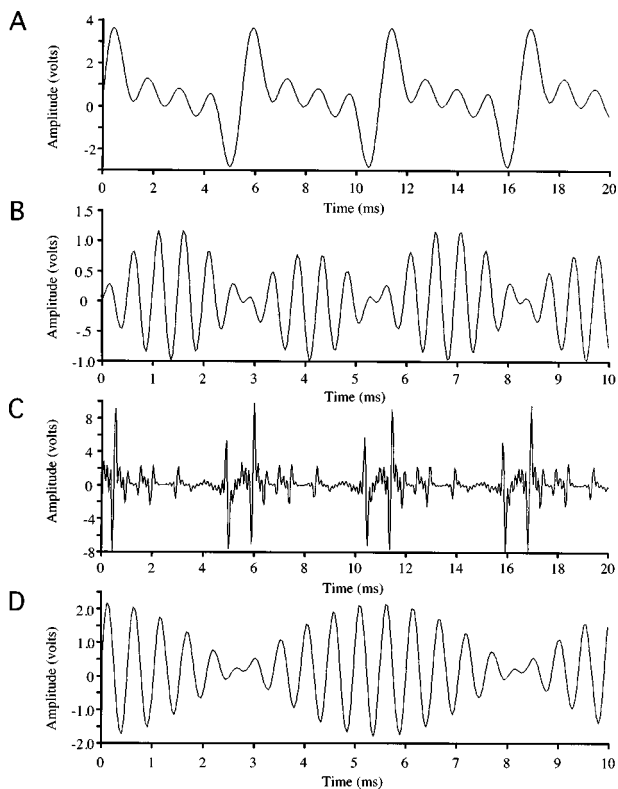
FIG. 2. Amplitude waveforms generated electronically using SIGNAL sound-analysis software (Beeman, 1996). (A) The harmonic signal generated by adding four sinusoidal signals (183, 366, 549, and 732 Hz), each with a 0.1-mV dc component (Bradbury and Vehrencamp, 1998) and an initial amplitude of 1.0 V. (B) The amplitude-modulated signal generated by multiplying two sinusoidal signals (183 and 2017 Hz), each with a 0.1-mV dc component and an initial amplitude of 1.0 V. (C) The amplitude-modulated signal generated by multiplying two multi-frequency harmonic signals (183 Hz with 4 harmonics and 2017 Hz with 3 harmonics), each with a 0.1-mV dc component and an initial amplitude of 1.0 V. (D) The beat signal generated by adding together two sinusoidal signals (1822 and 2005 Hz), each with a 0.1-mV dc component and an initial amplitude of 1.0 V.
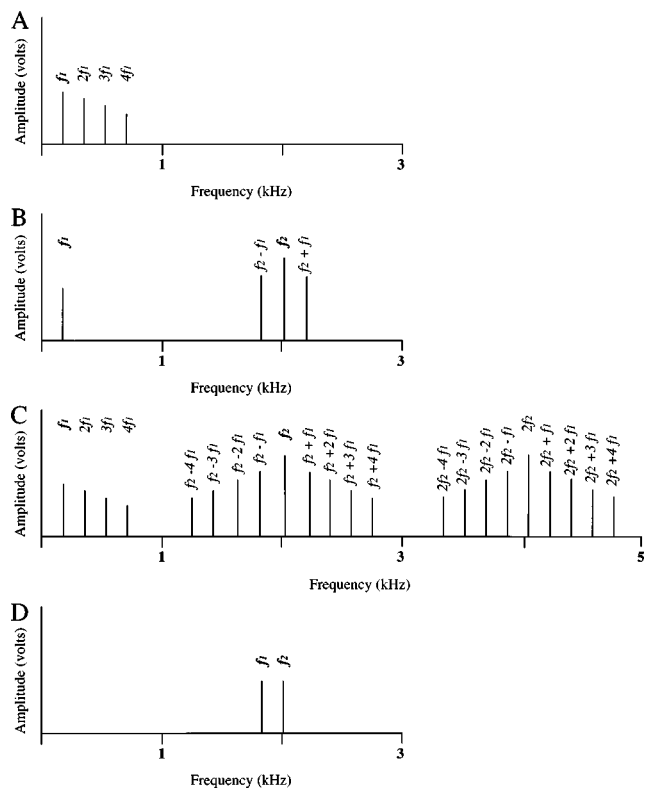

FIG. 3. Schematic Fourier power spectra for signals illustrated in Fig. 2. (A) Power spectrum of the multi-frequency harmonic signal of Fig. 2(A). The fundamental repeating unit, or fundamental frequency, is designated by the f_1 component at 183 Hz. Spacing between each component in the spectrum is also 183 Hz, and each component is found at an integral multiple of 183 Hz (e.g., 366, 549, and 732 Hz). (B) Power spectrum of the amplitude-modulated signal of Fig. 2(B). dc components in both original signals are signified by component frequencies in the spectrum that represent the fundamental frequencies of both input signals, f_1 and f_2 (183 and 2017 Hz, respectively). Sidebands occur at $f_2 - f_1$ and $f_2 + f_1$. (C) Power spectrum of the amplitude-modulated signal of Fig. 2(C). dc components in both original signals are signified by component frequencies in the spectrum at f_1 and f_2 (183 and 2017 Hz, respectively). The multi-frequency harmonic nature of both input signals is illustrated by the presence of numerous component frequencies at integral multiples of the modulating frequency, f_1, and multiple sidebands above and below the carrier frequency, f_2. A second harmonic of the carrier frequency is at $2f_2$ (4034 Hz), with numerous sidebands above and below it. A third harmonic of the carrier frequency would be at $3f_2$ (6051 Hz), with its full complement of sidebands, but is omitted for clarity. (D) Power spectrum of the beat signal of Fig. 1(D). This spectrum shows that the beat signal is generated from the linear interaction (addition) of two input signals: The only two components in the spectrum are those of the original input signals, f_1 and f_2 (1822 and 2005 Hz, respectively).

frequency modulating signal. Because modulation is a nonlinear process (modeled by multiplication of sinusoids represented by polynomials, see below), interactions between the carrier and modulating signals create new frequencies not present in either initial signal. When subject to Fourier transformation, the new components are represented as heterodyne sidebands (sum and difference frequencies) in the spectrum. Thus, two source signals (periodic or aperiodic) interact nonlinearly to produce a resultant output waveform that is not a harmonic series (i.e., it has no single fundamental frequency), and should not be represented by a harmonic array of components. The Fourier spectrum contains a set of component frequencies that, when summed, produce the observed waveform, but those components are not integer multiples of a fundamental frequency. Ascribing their origin to a simple harmonic process is incorrect and misleading regarding the acoustic nature of the signal and the physical nature of the source.

The process of amplitude modulation is not synonymous or analogous to the simple variation in amplitude of a signal with time that can be observed in a display of the gross temporal envelope [Fig. 1(A)]. Such modulations may or may not be due to the nonlinear process of amplitude modu-lation, but no conclusions can be drawn from this level of analysis. Amplitude modulation occurs uniquely when two signals interact nonlinearly and as a result produce new heterodyne sideband components and a waveform that increases and decreases in amplitude. Some linear processes (e.g., simple summation that occurs during beating), can also produce a waveform that appears modulated in amplitude (see below), but do not produce the physical phenomenon of amplitude modulation nor the new heterodyne sideband components. Thus, the presence of a modulated-amplitude waveform may indicate, but is not conclusive evidence of, an amplitude modulation process. That verification requires detailed analysis of the frequency composition of the Fourier spectrum.

Mathematically, frequencies that result from the nonlinear process of amplitude modulation can be predicted by multiplying the two original input signals. The exact spectral composition of the final output signal depends on two critical features: (1) whether the carrier and/or modulating signals are single frequency (i.e., pure tone) or multi-frequency harmonic signals; and (2) whether a direct current (dc) component exists in either signal. (Note: dc components are typically generated by a unidirectional air flow past a sound-generating organ. All voiced vocalizations, such as the vowel sounds and contact calls discussed here, thus have a dc component manifest in the spectrum as an energy component at zero Hz; Bradbury and Vehrencamp, 1998.) Consider a sound constructed from single-frequency harmonic carrier and modulating signals, each with a dc component, described by two sine waves with the formulas

Modulating Signal=signal 1:$v_1(t)=A+B \cos 2\pi f_1 t$,

Carrier Signal=signal 2:$v_2(t)=C+D \cos 2\pi f_2 t$,

where f_2 and f_1 are the carrier and modulating signals, respectively, and $f_2 \geqslant f_1$; A and C represent the dc components of each signal, and B and D the amplitudes. For simplicity, I omit the 2π symbol from subsequent equations. Multiplication of these two formulas yields

$$v_1(t) \times v_2(t)=AC+BC \cos f_1 t+AD \cos f_2 t$$
$$+BD \cos f_1 t \cos f_2 t. \qquad (1)$$

From simple geometric identity, two cosine terms may be represented as

$$\cos x * \cos y = 1/2 \cos(x+y)+1/2 \cos(x-y), \qquad (2)$$

so that the above equation is expressed as

$$v_1(t) \times v_2(t)=AC+BC \cos f_1 t+AD \cos f_2 t$$
$$+1/2 BD \cos(f_2+f_1)t$$
$$+1/2 BD \cos(f_2-f_1)t. \qquad (3)$$

Equation (3) provides terms for the features defining an amplitude-modulated process: First, both the carrier (f_2) and the modulating (f_1) signals are present in the output signal, albeit with altered amplitudes, and are thus identifiable by their distinct component frequencies in the spectrum. Second, two sum and difference frequencies are generated that were not present in either input signal, and are found in the spectrum equidistant above and below the carrier signal, at f_2+f_1 and f_2-f_1. These frequencies, or sidebands, create a spectrum characteristic of amplitude-modulated signals with energy distributed symmetrically on either side of the carrier signal (Nowicki and Capranica, 1986a, b; Bradbury and Vehrencamp, 1998). The presence of the original input signals, f_1 and f_2, in the output signal depends upon the existence of dc components associated with each input signal. If neither input signal has a dc component (if $A=C=0$), then only the sum and difference frequencies (f_2+f_1 and f_2-f_1) are produced. If f_1 but not f_2 has a dc component, only f_2 will be in the output signal, etc. Determining amplitudes of each output component is theoretically possible from the mathematical equations; practically, the exact amplitude of each independent input signal is difficult to determine for a biological signal (unless measured just above the source[s]). I thus do not further discuss amplitude values for spectral components.

Figure 2(B) shows an amplitude waveform, and Fig. 3(B) the spectral frequencies generated by multiplying two single-frequency harmonic signals, one at 2017 Hz and one at 183 Hz, each with a dc component. Both signals are represented in the output signal waveform, and direct measure of the waveform yields components that correspond to the fundamental frequencies of the carrier and modulating signals: In Fig. 2(B), the 2017-Hz frequency is clearly identifiable, and is modulated in amplitude at a rate of 183 Hz, producing the characteristic amplitude-modulated waveform envelope. In Fig. 3(B), the 2017-Hz frequency is represented by a centrally located component surrounded on either side by components at 183-Hz intervals; note the four spectral components at the mathematically predicted frequencies: f_1, f_2, f_2-f_1, and f_2+f_1.

Consider now two multi-frequency harmonic signals, each with a dc component:

Modulating Signal=signal 1:

$$v_1(t)=A+B_1 \cos f_1 t+B_2 \cos 2f_1 t+\cdots,$$
$$+B_m \cos mf_1 t,$$

Carrier Signal=signal 2:

$$v_2(t)=C+D_1 \cos f_2 t+D_2 \cos 2f_2 t+\cdots,$$
$$+D_n \cos nf_2 t,$$

where $f_2 \geqslant f_1$, m and n are integers (1,2,3,...) representing the harmonics of each multifrequency signal, A and C are the dc components, and B and D the amplitudes.

Multiplication of these two signals yields

$$v_1(t) \times v_2(t)=AC+B_1 C \cos f_1 t+AD_1 \cos f_2 t$$
$$+1/2B_1 D_1 \cos(f_2+f_1)t+1/2B_1 D_1 \cos(f_2$$
$$-f_1)t+CB_2 \cos 2f_1 t+1/2B_2 D_1 \cos(f_2$$
$$+2f_1)t+1/2B_2 D_1 \cos(f_2-2f_1)t$$
$$+AD_2 \cos 2f_2 t+1/2B_1 D_2 \cos(2f_2+f_1)t$$
$$+1/2B_1 D_2 \cos(2f_2-f_1)t+\cdots. \qquad (4)$$

Equation (4) provides terms for three defining features of this type of amplitude modulated signal: First, because each input signal has a dc component, components that correspond to the fundamental frequencies of both the carrier (f_2) and modulating (f_1) signals are present in the output signal, and are represented by components at these frequencies in Fig. 3(C). Second, output signal components at frequencies corresponding to harmonics of each input signal occur at integer multiples of the input signals (i.e., $CB_m \cos mf_1 t$, $AD_n \cos nf_2 t$). Third, sum and difference frequencies corresponding to each cross-product, $1/2B_m D_n \cos(nf_2+mf_1)t$ and $1/2B_m D_n \cos(nf_2-mf_1)t$, produce multiple sidebands, spaced mf_1 Hz above and below each integer multiple of the carrier signal. These sideband frequencies are again products of the nonlinear multiplica-

tion process of amplitude modulation, and are not in the original input signals.

Figures 2(C) and 3(C) show the complex amplitude waveforms and spectral frequencies generated by multiplying two multifrequency harmonic signals with fundamental frequencies of 2017 Hz (with 3 harmonics) and 183 Hz (with 4 harmonics), respectively, each with a dc component [using Eq. (4)]. In Fig. 3(C), note the components that correspond to fundamental frequencies and harmonics of the original input signals (f_1 and f_2, mf_1 and nf_2, respectively), and the multiple sidebands above and below each harmonic of f_2.

When discussing amplitude-modulated signals, terms such as ''fundamental frequency'' and ''harmonic(s)'' are neither appropriate nor correct. An amplitude-modulated signal is not a harmonic signal: It has no fundamental frequency nor harmonics of that fundamental. Although the terms fundamental frequency and harmonic may be appropriate, and even helpful, for describing the separate carrier and modulating signals, they are not appropriate for describing the resultant amplitude-modulated signal. In the above explanations, I have used these terms only to describe how specific components of an amplitude-modulated spectrum arise.

3. Beating

Beating occurs when two signals sum (a linear interaction). Beating (e.g., between signals of 2005 and 1822 Hz), produces a waveform that waxes and wanes in amplitude periodically, thus resembling an amplitude-modulated signal [compare Fig. 2(B) and (D)]. The rate at which the envelope of this amplitude waveform ''beats'' (or waxes and wanes) equals the difference between the two signals (here, 183 Hz). Fourier spectra of signals produced by beating and amplitude modulation, however, are very different [compare Fig. 3(B) and (D)]. The Fourier spectrum of a beat signal contains components at, and only at, the exact frequencies of the two original signals, in contrast to the sum and difference frequencies produced by amplitude modulation. Although beating can also create what are known as difference or combination tones (i.e., perception of a 183-Hz signal), these tones are perceptual illusions produced solely by nonlinearities in auditory or neural systems of the receiver. These tones are not part of the output waveform (Roederer, 1995), and thus not represented in the Fourier spectrum.

C. The current study

Acoustic evidence for the presence of amplitude modulation in both budgerigar contact calls and English vowel productions is presented below. In the discussion that follows, implications of the presence of amplitude modulation are considered, specifically with respect to the ontogeny of budgerigar vocalizations, and the neural and mechanical bases of vocal production in budgerigars.

I. METHODS

A. Subjects

I present vocalizations from four male budgerigars. Three birds, Buddy, Forest, and Frans, were removed from a breeding aviary at fledging (4–5 weeks) and subsequently trained to produce human vocalizations. Buddy and Forest were housed alone in cages, but in auditory and visual contact with humans and other birds. Frans was housed in a soundproof isolation box, with little auditory or visual contact with other birds. Frans had at least 1 h of human interaction 5–6 days/week, and was exposed to auditory tapes (of either a human reading or soft classical and easy-listening music) for 6–8 h/day. A fourth male, M03, neither hand-raised nor trained on English vocalizations, was obtained from a commercial breeding flock and subsequently caged with 11 other budgerigars in various combinations (two–five birds at a time). All birds received food and water *ad libitum*. M03's conspecific vocalizations allowed comparisons between flock-reared and human-reared birds (i.e., Buddy, Forest, and Frans).

B. Training of English vocalizations

Buddy, Forest, and Frans were exposed to and trained to produce English words and phrases via the Model/Rival (M/R) technique (Todt, 1975; Pepperberg, 1981), or a modified version (using only one trainer; Banta and Pepperberg, 1995; Banta, 1998). Each bird was trained for ~1 h/day, 5–6 days/week, from about 6 weeks of age. Buddy, Frans, and Forest were recorded in the laboratory during training and while vocalizing freely on a perch or in their cage when they were fully adult (at least 6 months old), and when the target vocalization was produced in a clear and stable manner. Target vocalizations were single words and phrases, e.g., ''paper,'' ''cork,'' ''wood,'' ''bear,'' and ''truck.'' Birds also acquired vocalizations used during training and social interactions, e.g., ''kiss,'' ''climb,'' ''tickle,'' ''you're right,'' ''good boy,'' ''okay,'' and ''come here.'' The primary tutors for Buddy, Forest, and Frans were humans, but all three birds were at times in auditory contact with other birds (both budgerigars and Gray parrots); thus, they may have also learned some vocalizations from other birds. M03 received no formal human tutoring.

C. Audio recordings

Vocalizations were recorded on Maxell XLII audio tapes with a Sony TCM 5000 tape recorder and AKG C541 EB, Sennheiser ME 66, or Sennheiser ME 67 microphones. M03 was recorded while isolated in his cage. M03's and human (PB's) vocalizations were recorded with Fuji DR-II audio tapes on a Marantz PMD221 portable cassette recorder, and with an Audio-Technica AT835b condenser microphone.

D. Acoustic analyses

Acoustic analysis methods were as follows: Frans' and Forest's vocalizations were filtered at <400 Hz and at >10 000 Hz with a Hewlett-Packard bandpass filter (model 8056A). Buddy's vocalizations were produced at a greater amplitude, and contained less background noise than those of the other birds (he often sat closer to the microphone and preferred to vocalize when it was quiet), and thus did not require filtering. Frans' and Forest's recordings were digitized with a Kay Elemetrics 5500 DSP sona-graph (20 480

Hz sampling rate, 8-kHz frequency range). Buddy's, M03's, and PB's recordings were digitized with SIGNAL (Beeman, 1996) sound-analysis software (25 000-Hz sampling rate, 8-kHz frequency range). M03's and PB's vocalizations were first alias filtered above 10 000 Hz. Spectra and amplitude waveforms were analyzed on the Kay and with SIGNAL. For English words, 40-ms sections of vowels were isolated and analyzed; for contact calls, entire vocalizations and sections of various lengths (see Sec. II) were analyzed. Power spectra were calculated with a 1024-point transform length that resulted in 20-Hz resolution for the vocalizations of Frans and Forest, and 24.4-Hz resolution for the vocalizations of Buddy, M03, and PB (differences in frequency resolution are due to differences in sampling rate). Spectrograms were calculated with various transform lengths (see Sec. II).

II. RESULTS

A. Budgerigar contact calls exhibit amplitude modulation

Figure 4(A)–(D) show wide- and narrow-band spectrograms, a power spectrum, and an amplitude waveform, respectively, from flock-reared M03's contact call. Note the harmonic-like stack of component frequencies in the spectrograms in the region demarcated by the time cursors [Fig. 4(A),(B)]. A 1024-point power spectrum of the last 10 ms of this region [82–92 ms, where the stack occurs; Fig. 4(C)] also reveals a harmonic-like spectrum, with energy components at apparently regular intervals from 723–6973 Hz. In the spectrum, however, the maximal energy occurs at 3106, not 723, Hz. Moreover, although the first and second component frequencies at 723 and 1484 Hz are integer or near-integer multiples of 742 Hz (0.97 and 2.0, respectively), none of the other spectral components is an integer multiple of 742 Hz (e.g., 3106/742=4.186), a pattern inconsistent with a harmonic signal. Instead, energy components are evenly spaced at 742 Hz on either side of 3106 Hz, a pattern consistent with an amplitude-modulated signal having a dominant (i.e., component with greatest energy) or carrier signal of 3106 Hz. Also, an integer multiple of this dominant component (corresponding to the second harmonic of the carrier frequency) can be identified at 6211 Hz (6211/3106 =2.000), as a local energy peak with components located nearly symmetrically 723 Hz below and 762 Hz above this integer multiple component. If this vocalization were a harmonic series with a fundamental frequency of 3106 Hz, no other frequency components of significant energy would be found below the fundamental frequency or between the fundamental frequency and its second harmonic. At this point in M03's call, however, numerous components lie below this dominant component, and between the dominant component and its second harmonic, a pattern inconsistent with a harmonic signal.
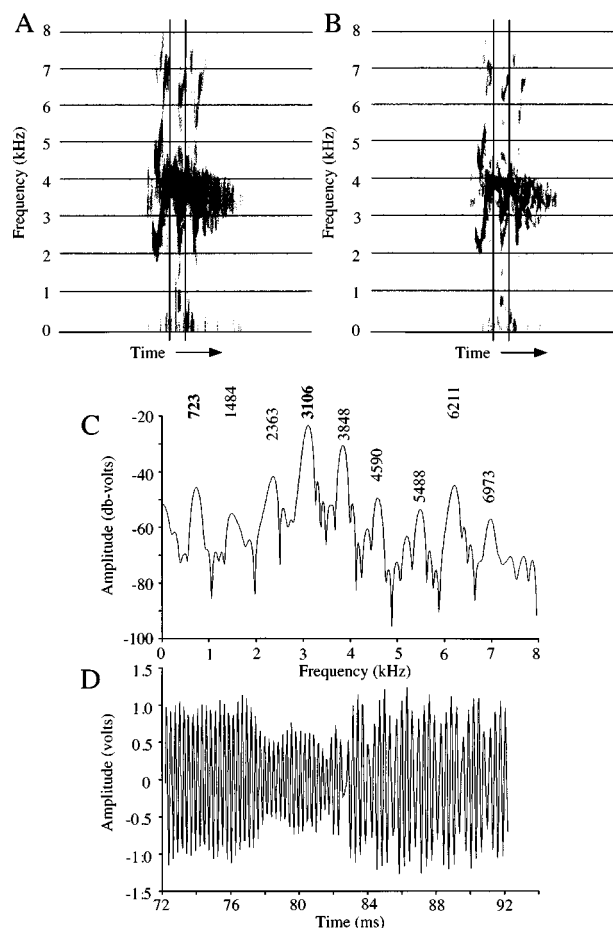

FIG. 4. M03's contact call. (A) Wideband spectrogram (500-Hz analysis filter). Time cursors demarcate the 20-ms section displayed in the amplitude waveform [(D)]. (B) Narrow-band spectrogram (150-Hz analysis filter). Time cursors demarcate the same region as in (A). (C) 1024-point power spectrum of the last 10-ms region of the waveform with periodic modulation in amplitude [(D), 82–92 ms]. The dominant component is at 3106 Hz, with components evenly spaced 742 Hz above and below. Components at 723 and 1484 Hz are at integral multiples of the modulating signal. (D) Amplitude waveform of the 20-ms period demarcated by cursors in (A) and (B), from which the 10-ms period for the power spectrum in (C) was taken. The dominant (carrier) signal measured directly from the last 10 ms of this waveform is 3349 ($\pm$94) Hz; the modulating signal is 717 ($\pm$67) Hz.

Direct inspection of the amplitude waveform [Fig. 4(D)], reveals a high-frequency signal modulated in amplitude at a much slower rate. The 20 ms of signal that precedes the stack of frequencies (only the last 10 ms shown) is characterized by a waveform of relatively constant frequency (~3850 Hz). At ~78 ms, amplitude of the oscillation decreases rapidly, but the waveform frequency remains constant. At ~83 ms, the waveform frequency drops slightly to 3349 ($\pm$94) Hz, and its amplitude begins to increase and decrease periodically, at a frequency of 717 ($\pm$67) Hz. Both the dominant frequency and rate of modulation in the waveform correspond well to the dominant frequency component (3106 Hz) and the intervals between components (742 Hz) in the spectrum, respectively, corroborating that the spectrum corresponds to an amplitude-modulated signal.

Of particular interest in this vocalization is the upper sideband at 3848 Hz [Fig. 4(C)], which is nearly identical to the dominant frequency of the portion of the signal immediately preceding this amplitude-modulated segment (at
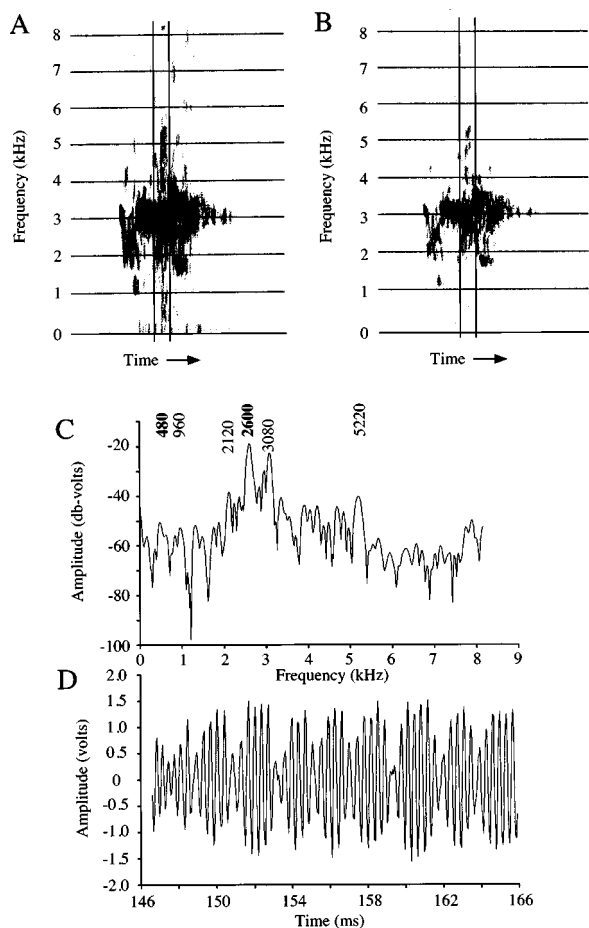
FIG. 5. Forest's contact call. (A) Wideband spectrogram (300-Hz analysis filter) of the call in Fig. 3. Time cursors demarcate the 20-ms section displayed in the amplitude waveform and analyzed in the power spectrum. (B) Narrow-band spectrogram (150-Hz analysis filter). Time cursors demarcate the same region as in (A). (C) 1024-point power spectrum of the 20-ms region demarcated by cursors in (A) and (B). Note the dominant component at 2600 Hz, and components evenly spaced 480 Hz above and below, and integral multiples of the modulating frequency at 480 and 960 Hz (D) Amplitude waveform for the 20-ms period demarcated by cursors in (A) and (B), on which the power spectrum was performed. The dominant (carrier) signal measured directly from this waveform is 2798 ($\pm$40) Hz; the modulating signal is 473 ($\pm$49) Hz.

$\sim$3850 Hz). Indeed, in the narrow-band spectrogram [Fig. 4(B)] the two segments appear almost continuous. This example demonstrates how an incorrect inference regarding the activity of the source (e.g., the frequencies produced) can arise when only the Fourier spectrum is analyzed.

Forest's contact calls (as well as those of seven of nine other budgerigars analyzed for nonlinear amplitude modulation to date) exhibit amplitude-modulation patterns similar to those of M03. Figure 1(A) shows the entire amplitude envelope of one of Forest's calls, and 1(B) an expanded section of time from that call. Note the extensive amplitude fluctuations throughout. Figure 5(A)–(D), respectively, show wide- and narrow-band spectrograms, the power spectrum, and another portion of the amplitude waveform from the call in Fig. 1. From 147–166 ms, the amplitude of the waveform [Fig. 5(D)] is modulated in a regular or periodic manner. Inspection of the wideband spectrogram at this point [Fig. 5(A), between the time cursors] reveals an apparent drop in fre-

quency of the dominant component, accompanied by a smear of energy that extends across a large span of frequencies (from $\sim$500–5500 Hz). Inspection of the narrow-band spectrogram [Fig. 5(B)] reveals several closely apposed component frequencies at apparently evenly spaced frequency intervals. A 1024-point power spectrum (of the 20 ms between the vertical lines) identifies the spectrum's dominant component at 2600 Hz, with components evenly distributed 480 Hz above and below this frequency, a pattern consistent with that of an amplitude-modulated signal. Components also exist at 480 and 960 Hz, but the dominant frequency, 2600 Hz, is *not* an integer multiple of 480 Hz (2600/480=5.4167); thus, this component is not simply a harmonic of a 480-Hz fundamental whose energy has been enhanced by suprasyringeal filtering. Energy at 480 and 960 Hz is consistent with components that correspond to the fundamental frequency of the modulating signal and its first integer multiple. Note the many spectral components between the carrier signal and its second harmonic (at 5220 Hz), a pattern inconsistent with that of a harmonic vocalization.

Inspection of the amplitude waveform of this section of the call [Fig. 5(D)] confirms that the spectrum is generated by an amplitude-modulated signal. Direct measure of the waveform reveals a 473 ($\pm$49)-Hz modulation superimposed upon the dominant 2798 ($\pm$40)-Hz signal. Both the dominant frequency and rate of modulation in the waveform correspond well with the dominant frequency component (2600 Hz) and the intervals between components (480 Hz) in the spectrum.

B. Human and budgerigar vowel spectra differ in their properties

When subject to Fourier analysis, most human vowels produce a quasi-harmonic spectrum consisting of a fundamental frequency and a stack of harmonic components, with each component located at an integer or near-integer multiple of the fundamental frequency (the fundamental of a human vowel is the frequency at which the vocal folds, or larynx, vibrate open and closed). Figure 6(A) and (B) show wide- and narrow-band spectrograms of a typical harmonic human vocalization, PB's "bear" (produced with the same intonation as used when training budgerigars). A power spectrum [Fig. 6(C)] of the /er/ sound reveals a fundamental frequency of 220 Hz, and harmonics at integer or near-integer multiples of the fundamental (i.e., 440, 659 Hz, etc.). Direct measure of the amplitude waveform [Fig. 6(D)] yields a fundamental frequency of 221 ($\pm$2) Hz (i.e., the waveform repeats every 4.5–4.6 ms).

Budgerigar vowel spectra (Figs. 7–9), in contrast, possess features of amplitude-modulated rather than harmonic signals. When represented via Fourier analysis, budgerigar vowel sounds possess a complex array of frequency components. The greatest spectral energy occurs in the middle of a group of components with significant energy distributed symmetrically on either side of this local maximum.

A 1024-point power spectrum [Fig. 7(C)] of a 40-ms section (155 to 195 ms) of Frans' /er/ in "bear" revealed that the maximal energy was at 1840 Hz, with component frequencies 100 Hz below and 40 Hz above the 1840-Hz
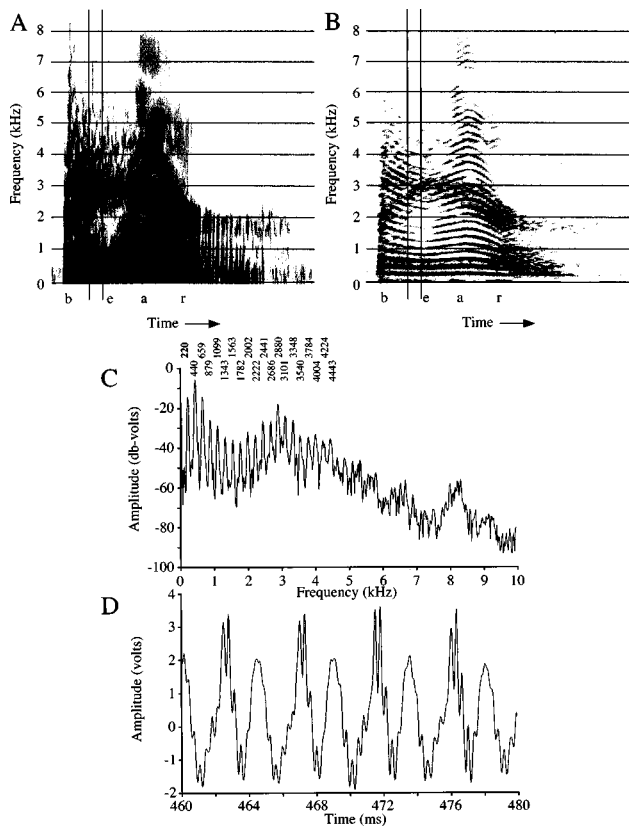
FIG. 6. A human's (PB's) production of "bear." (A) Wideband spectrogram (300-Hz analysis filter). Time cursors demarcate a 40-ms section (450–490 ms). (B) Narrow-band spectrogram (45-Hz analysis filter). Time cursors demarcate the same region as in (A). (C) 1024-point power spectrum of the 40-ms section demarcated in (A) and (B). Note the integrally spaced harmonics. The fundamental frequency determined from the power spectrum is 220 Hz. In this vocalization, the component with the greatest energy is the second harmonic. (D) Amplitude waveform of a 20-ms portion of the 40-ms section demarcated by cursors in (A) and (B). The fundamental frequency determined from direct measure of the waveform is 222 (±2) Hz.
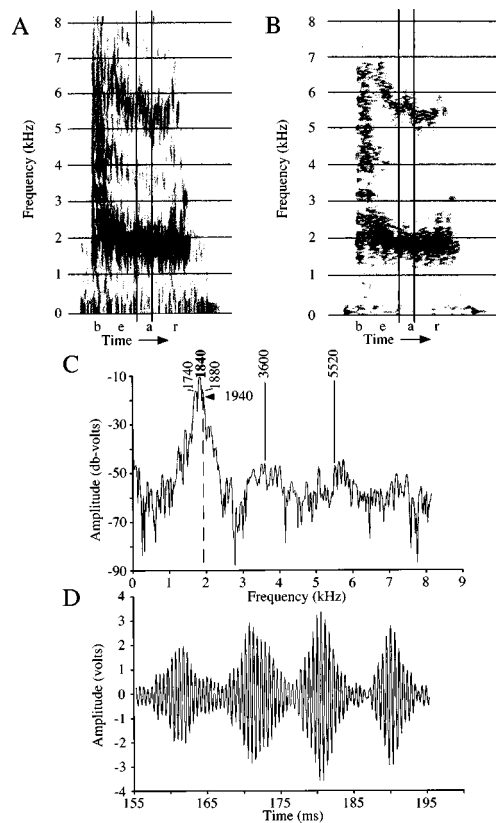
FIG. 7. Frans' production of "bear." (A) Wideband spectrogram (300-Hz analysis filter). Time cursors demarcate a 40-ms section (450–490 ms). Components are located at integral multiples of the carrier frequency (3600 and 5220 Hz). (B) Narrow-band spectrogram (45-Hz analysis filter). Time cursors demarcate the same region as (A). (C) 1024-point power spectrum of the 40-ms section demarcated in (A) and (B). The dominant frequency identified in the power spectrum is 1840 Hz. Component frequencies are 100 Hz below and 40 Hz above the dominant frequency (at 1740 and 1880 Hz, respectively), but significant energy is in the spectrum at 1940 Hz (100 Hz above the carrier signal, where the dashed line and the spectrum intersect). (D) Amplitude waveform of the 40-ms section demarcated by cursors in (A) and (B). Direct measure of the amplitude waveform yielded a carrier signal of 1866 (±12) Hz, and a modulating frequency of 100 (±2) Hz.

frequency. Direct measure of frequencies in the amplitude waveform [in Fig. 7(D), from the peak of one high-frequency period to the next, or from the first peak of one slow-frequency period to the first peak of the next] yielded a dominant frequency of 1866 (±12) Hz, and a modulating frequency of 100 (±2) Hz. Returning to the spectrum, the lower 1740-Hz sideband occurs exactly where predicted (100 Hz below 1840 Hz), but the upper sideband at 1880 Hz is not 100 Hz above the carrier frequency. Note, however, the significant energy at 1940 Hz [e.g., 100 Hz above 1840 Hz; Fig. 7(C)], possibly reflecting the presence of an upper sideband at 1940 Hz that is obscured by another energy component at 1880 Hz. This possibility is discussed in greater detail below.

Thus, evidence from signal analyses suggest that Frans' /er/ vowel sound is produced by amplitude modulation. The dominant frequency identified in the waveform [Fig. 7(D)] contains the greatest energy of all components in the spectrum [Fig. 7(C)], and is surrounded on either side by energy components [Fig. 7(C)], two defining characteristics of an amplitude-modulated signal. The 1840–1866-Hz signal is the carrier; the 100-Hz signal is the modulating signal. Note the second and third integral multiples of the carrier signal near 3680 and 5520 Hz, indicating that the carrier is a mul-

tifrequency harmonic signal. The presence of the carrier signal in the spectrum indicates that the modulating signal has a dc component.

Frans' /er/ amplitude waveform envelope [Fig. 7(D)] resembles that of a classically amplitude-modulated signal. Such appearance suggests but is not definitive evidence for amplitude modulation. As described above, beating can produce a similar amplitude envelope, but a very different Fourier spectrum. For budgerigar vowel spectra, component frequencies occur symmetrically around the frequency with the greatest energy, an attribute consistent with a spectrum generated by an amplitude-modulated signal, not by beating [compare Fig. 3(B) and (C) with Fig. 3(D)].

Buddy's /er/ in "bear" (Fig. 8) produces a similar spectrum. A 1024-point power spectrum [Fig. 8(C)] identifies the component with maximal energy as 2656 Hz. Direct measure of the amplitude waveform yields a carrier signal of 2676 (±21) Hz and a modulating signal of 255 (±9) Hz. Frequency differences between adjacent components vary from 78–352 Hz, but numerous components are separated by 254 or 273 Hz, values close to that of the modulating signal
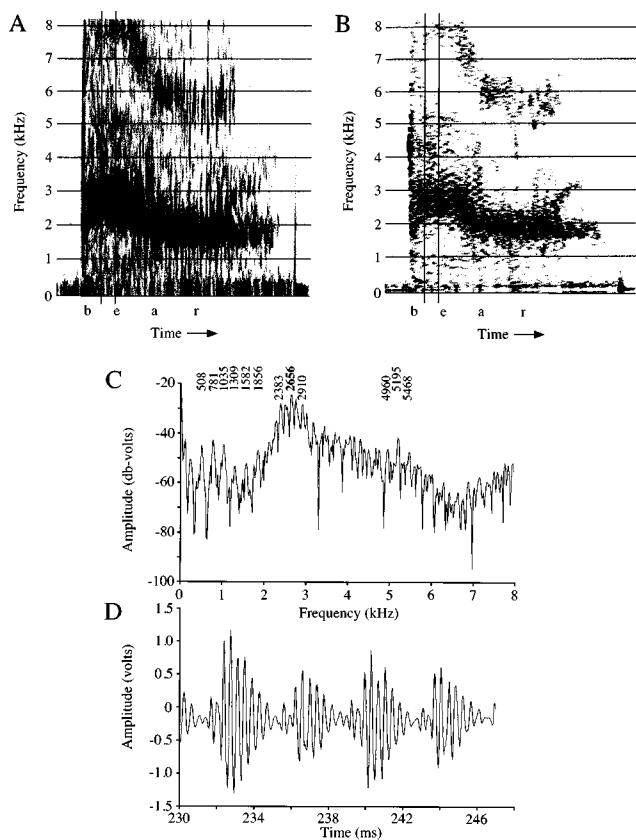
FIG. 8. Buddy's production of ''bear.'' (A) Wideband spectrogram (300-Hz analysis filter). Time cursors demarcate a 40-ms section (220–260 ms). Components are located at integral multiples of the carrier frequency (5195 and ~8000 Hz). (B) Narrow-band spectrogram (45-Hz analysis filter). Time cursors demarcate the same region as in (A). (C) 1024-point power spectrum of the 40-ms section demarcated in (A) and (B). The dominant frequency identified in the power spectrum is 2656 Hz. Component frequencies are 273 Hz below and 254 Hz above the dominant frequency (at 2383 and 2910 Hz, respectively), but other components exist between those components (at 2481 and 2754 Hz, respectively). (D) Amplitude waveform of 18 ms of the 40-ms section demarcated by cursors in (A) and (B). Direct measure of the amplitude waveform yielded a carrier frequency of 2676 (±21) Hz, and a modulating frequency of 254 (±9) Hz.

FIG. 9. Forest's production of ''okay.'' (A) Wideband spectrogram (300-Hz analysis filter). Time cursors demarcate a 40-ms section (40–80 ms) of the /o/. Note how low-frequency components extend in time beyond the region of the sound with the majority of energy (below arrowheads). (B) Narrow-band spectrogram (45-Hz analysis filter). Time cursors demarcate the same region as in (A). (C) 1024-point power spectrum of the 40-ms section demarcated in (A) and (B). The dominant frequency in the power spectrum is 3980 Hz. Numerous components are separated by either 260 or 280 Hz, including the components that are two below (at 3700 Hz) and two above (at 4240 Hz) the carrier signal. (D) Amplitude waveform of 8 ms of the 40-ms section demarcated by the cursors in (A) and (B). Direct measure of the amplitude waveform yielded a carrier signal of 4617 (±295) Hz, and a modulating signal of 279 (±21) Hz.

derived from the amplitude waveform. The component two bands below the 2656-Hz component is separated from it by 273 Hz; the component two bands above the 2656-Hz component is separated by 254 Hz. At lower frequencies (this vocalization was not filtered), a harmonic-looking series of components is separated by either 254 or 273 Hz. These components appear to be integer multiples of the fundamental frequency of the modulating signal and thus indicate a dc component in the carrier, and a multifrequency harmonic modulating signal. The second integer multiple of the carrier is visible at 5195 Hz (5195/2656=1.96), indicating its multifrequency harmonic nature. Note also the sidebands 235 Hz below and 273 Hz above the 5195-Hz component. Numerous frequency components exist between the first and second harmonics of the carrier, a pattern inconsistent with a harmonic vocalization.

Figure 9 shows Forest's ''o'' from ''okay.'' Spectral components of this sound are consistent with properties of an amplitude-modulated signal: (1) components corresponding to the fundamental of the carrier signal (3980 Hz) and integer multiples of the modulating signal are present (the funda-
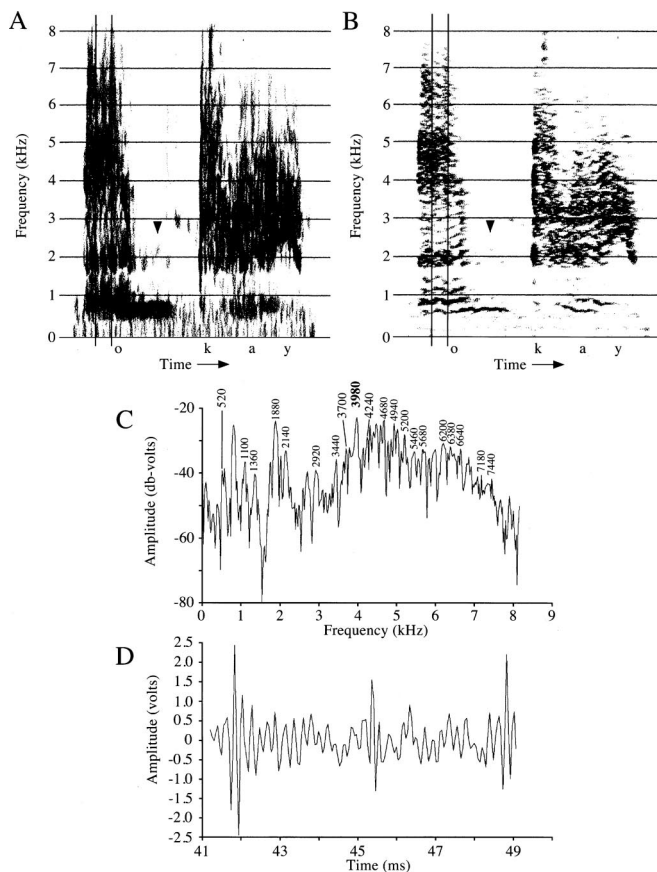
mental of the modulating signal is 260 Hz, but its first visible component is 520 Hz because of filtering <400 Hz); (2) numerous integer multiples of the modulating signal indicate its multifrequency harmonic nature (Note: the 8000-Hz sampling range eliminates a second integer multiple of the carrier signal); and (3) numerous energy bands on both sides of the carrier signal are visible, many of which are separated by either 260 or 280 Hz.

Measurements of the amplitude waveform concur with frequencies in the spectrum. The modulating signal, at 279 (±21) Hz, corresponds to the 260–280-Hz modulating signal identified in the spectrum. The carrier signal identified in the amplitude waveform, at 4617 (±295) Hz, differs more (although only by 14%) from the 3980 Hz derived from the power spectrum than did these estimations in other birds. When the amplitude waveform is as drastically modulated in amplitude as in this bird's vocalization, however, difficulties arise during wave shape analysis in distinguishing peaks of

the carrier signal from what may be small energy peaks generated by harmonics or vocal-tract resonances of the carrier or modulating signals, or by spurious background noise.

Two other features are of particular interest in this "o" sound. First, note [Fig. 9(D)] the striking similarity of the shape and pattern of modulation of the amplitude waveform of this vocalization and the synthesized amplitude-modulated signal [Fig. 2(C)]. Second, note how several low-frequency components in the spectrograms [beneath arrowheads, Fig. 9(A) and (B)] extend in time beyond the portion of sound containing the broad spectrum of frequencies. A 1024-point power spectrum of this region of the vocalization (200–240 ms) reveals a dominant component at 610 Hz. Direct measure of the amplitude waveform yields a dominant frequency of 628 Hz. In this region of the vocalization, the carrier signal apparently ceases, and only what previously was the modulating signal continues to be produced. The actual fundamental frequency in this region may be 305 Hz, but pre-analysis filtering <400 Hz may have removed the energy at the fundamental. This hypothesis is supported by the presence of four other apparently harmonic components that extend up to 2167 Hz, and that are spaced at integer or near-integer multiples of 305 Hz [i.e., Fig. 9(B), components at 915, 1267, 1909, and 2165 Hz]. This phenomenon was observed in samples of other budgerigar vocalizations, and provides further evidence for the presence of two separate and independent frequencies.

For numerous budgerigar vowel sounds (and all budgerigar vocalizations described above), I calculated the carrier- and modulating-signal periodicity directly from the amplitude waveform. Pitch-synchronous spectrum analyses verified that the carrier signal is not an integer multiple (i.e., a harmonic) of the modulating signal (i.e., carrier signal/modulating signal ≠ an integer). These results further support the conclusion that the carrier and modulating signals are not harmonically related.

Finally, I analyzed both budgerigar vowels and amplitude-modulated regions of contact calls for the presence of frequency modulation. Periodic frequency modulations are also capable of producing discrete sidebands (Marler, 1969). Budgerigar vocalizations clearly exhibit frequency modulations in the form of both slow and rapid transitions of the carrier signal frequency (e.g., from one frequency to another). For example, as described above, M03s contact call exhibits a rapid transition from ~3850 to ~3349 Hz at ~83 ms in the call [Fig. 4(D)]. It is thus possible that periodic frequency modulations (e.g., periodic increases and decreases of the dominant signal) within each modulating period are responsible for the production of sideband components. My analyses showed, however, that frequency modulations of the carrier signal within single modulated periods are aperiodic modulations rather than periodic modulations (data not presented). The carrier frequencies of budgerigar vocalizations do not systematically increase, decrease, or increase and decrease in frequency within periods of the modulating envelope, but rather fluctuate around the carrier signal "target" frequency (the dominant frequency that the bird is attempting to produce). Furthermore, the period-to-period frequency of the carrier signal is not corre-

lated with the peak-to-trough amplitude of the waveform (data not shown). Periodic-frequency modulation is thus not responsible for producing the discrete sideband components of budgerigar vocalization spectra.

III. DISCUSSION

A. Budgerigar vocalizations contain amplitude modulation

Evidence presented here supports the conclusion that some portions of the acoustic spectra generated by budgerigar vocalizations arise from the nonlinear process of amplitude modulation. Note, however, that not all budgerigar vocalizations exhibit the nonlinear phenomenon of amplitude modulation responsible for creating sideband frequencies (e.g., budgerigar productions of English consonants and perhaps some warble-song elements; Note: many warble song elements are clicks or buzzes which are neither harmonic nor amplitude-modulated signals). Furthermore, amplitude modulation that creates discrete sidebands is not necessarily present or obvious throughout entire vocalizations (e.g., regions within contact calls where amplitude remains relatively constant, or fluctuates aperiodically). Thus, although entire budgerigar vocalizations may not exhibit all of the key features of amplitude modulation, these features are exhibited in portions of contact calls and in learned English vowel sounds. These key features include:

(1) Vocalizations with acoustic spectra that do not conform to those produced by harmonic vocalizations. These vocalizations do not have a dominant component at what would be the predicted fundamental frequency, and calculations fail to yield either a common or a plausible fundamental frequency. Furthermore, the frequency component in the spectrum with greatest energy is not an integer or near-integer multiple of any plausible fundamental.

(2) Acoustic spectra that contain a centrally located dominant component surrounded on each side by relatively symmetrical sidebands that, collectively, represent most of the energy in the signal.

(3) Two separate periodic, or almost-periodic, signals that are identifiable in the amplitude waveform and that accurately reflect frequencies of the carrier and modulating signals identified in the spectrum. The higher-frequency carrier signal in the waveform corresponds to the dominant frequency identified in the spectrum, and the lower-frequency modulating signal in the waveform corresponds to the frequency difference between many components in the spectrum.

(4) These two separate frequencies are not integrally related (i.e., the carrier signal is not an integer multiple of the modulating signal).

(5) A localized prominent component (compared to surrounding component amplitudes) occurs at a frequency twice that of the central dominant component (i.e., an integer multiple of the fundamental frequency of the carrier signal). This component is likewise surrounded lo-

cally by a pattern of energy, consistent with sidebands in an amplitude-modulated signal.

Amplitude modulation is evident in budgerigar productions of English vowel sounds. As mentioned above, budgerigar vowel spectra contain a centrally located dominant component and numerous sideband components separated by a frequency similar to the modulating frequency (determined from the waveform). At times, however, particular sideband components can be difficult to identify definitively because they occur at positions not predicted by the modulating frequency [e.g., the 1880-Hz component in Frans' /er/ in ''bear,'' Fig. 7(C)]. Possible reasons for this inconsistency are discussed below.

For budgerigar calls, the presence of a gross temporal envelope [Fig. 1(A)] and an amplitude waveform [Fig. 1(B)] that fluctuates in amplitude is obvious [this is the case for the calls of all (more than 16) budgerigars examined to date]. However, only isolated regions of calls (e.g., approximately 10%–20% of the duration) exhibit periodic amplitude modulation [Figs. 4(D), 5(D)]. At these points, the vocalization spectrum changes drastically, and sideband components are detectable. Thus, evidence in both the time domain (in the amplitude waveform) and in the frequency domain (in the Fourier spectrum) provide consistent verification of an underlying amplitude-modulation process in the generation of these isolated portions of budgerigar contact calls. The physical and acoustical processes responsible for producing the remainder of the call are, however, not yet known. Specifically, are the frequent, obvious fluctuations in the amplitude of the waveform throughout the rest of the call also produced by nonlinear amplitude modulation, or are they spurious fluctuations in amplitude?

B. Additional acoustic mechanisms and their influence on budgerigar vocalizations

1. The complexity of nonlinear amplitude modulation

As mentioned above, budgerigar vowel spectra also deviate somewhat from what is predicted by a simple model of amplitude modulation. One reason for this deviation is that components arising as integer multiples of the fundamental frequency of the modulating signal, and those generated as sidebands (i.e., components surrounding both the carrier and integer multiples of the carrier signal) may overlap in the spectrum. A simple example illustrates this phenomenon. Consider an amplitude-modulated signal with multifrequency harmonic carrier (2000 Hz) and modulating (300 Hz) signals. Integer multiples of the 300-Hz modulating signal would be found at 300, 600, 900, 1200, 1500, 1800, 2100 Hz, etc. The carrier signal produces a component at 2000 Hz, and sidebands would surround the carrier signal at 300-Hz intervals below (at 1700, 1400, 1100, 800, 500, 200 Hz) and above (at 2300, 2600, 2900 Hz, etc.) the carrier signal. Where the modulating and sideband components overlap, however, energy would occur at 200, 300, 500, 600, 800, 900, 1100, 1200, 1400, 1500, 1700, 1800, 2000, 2100, 2300 Hz, etc. (This phenomenon also occurs where sidebands of the carrier signal and its second integer multiple overlap.) This region in the spectrum would be difficult to interpret, as

it would consist of numerous closely apposed components separated by 100- and 200-Hz intervals, but not necessarily by the 300-Hz interval predicted by the modulating signal. (Note that such an array might be incorrectly interpreted to be a harmonic stack with a fundamental of 100 Hz, but with various missing harmonics.) Finally, depending on the window size of the Fourier transform, very closely apposed overlapping components may not be distinguishable, but rather may be represented as one single wideband component, further complicating the analysis. The described array of components resembles that of many budgerigar vowel spectra. By deriving specific information regarding both the carrier and modulating frequencies from the Fourier spectrum and amplitude waveform, however, the array can be identified as generated by the nonlinear process of amplitude modulation.

2. Suprasyringeal filtering

The contribution of suprasyringeal filtering to budgerigar vocalization spectra must also be considered. The present analyses cannot assess the role that the vocal tract plays to emphasize or de-emphasize frequencies created by the syrinx and other sound sources (if existent), but such filtering likely exists (Westneat *et al.*, 1993; Brittan-Powell *et al.*, 1997b). The budgerigar vocal tract likely emphasizes frequencies between 2000–4000 Hz (the dominant frequency range of contact calls; Dooling, 1986), thus emphasizing sidebands that occur near the carrier signal, but not those at other frequencies. Analyses of other budgerigar vowel productions (Banta, personal observation), suggest that budgerigars may also selectively emphasize components that occur above, while de-emphasizing or filtering out those that occur below, the carrier signal.

3. Aperiodic amplitude modulation

Inspection of the amplitude waveform for the major portion of any budgerigar call (i.e., in regions that do not exhibit an amplitude-modulated spectrum with discrete sidebands) reveals a waveform that appears to be modulated in amplitude aperiodically or chaotically [Fig. 1(B)]. Interestingly, nonlinear amplitude modulation that results from the interaction between a periodic carrier signal and an aperiodic modulating signal results in a much different spectrum than those presented in Fig. 3(B) and (C). Instead of producing a spectrum with discrete sidebands of energy (i.e., line spectra), an amplitude-modulated signal with a periodic carrier signal and an aperiodic modulating signal will have a large centrally located dominant component surrounded on either side by diffuse sideband energy that may be incorrectly hypothesized as arising from aperiodic frequency fluctuations or noise. The distance that this sideband energy extends on either side of the carrier signal is determined by the instantaneous rate at which the frequency of the modulating signal is fluctuating. Because the modulating signal can fluctuate in frequency very rapidly (e.g., with each period of the carrier signal for a chaotic modulating signal), Fourier transformation results in a ''smearing'' of the sideband energy with time, thus giving the spectrum a ''broadband'' or noisy ap-

pearance. Indeed, inspection of spectrograms from both M03's and Forest's calls [Figs. 4(A) and (B) and 5(A) and (B), respectively], reveal this broadband or noisy character.

4. Beating

The simple linear summation phenomenon known as beating cannot explain all of the spectral frequencies present in portions of budgerigar calls and budgerigar vowel sounds. Although beating can produce a waveform that is modulated in amplitude, its Fourier spectrum contains only the two original input frequencies. Even if beating occurred between two multi-frequency harmonic signals, the spectrum would not contain a centrally located dominant component surrounded symmetrically by other components. Such a spectrum results only from a nonlinear process such as amplitude modulation. Thus, the modulated waveform of budgerigar vowels and calls is not produced by beating.

5. Frequency modulation

Budgerigar vocalizations and their Fourier spectra are influenced by frequency modulations, but are not the product of periodic frequency modulation, which can also produce discrete line sidebands similar to those produced by periodic amplitude modulation (Marler, 1969). My analyses showed that periodic frequency modulations do not play a role in the production of discrete sidebands in the production of budgerigar vocalization spectra (data not presented). Frequency modulation, however, may contribute to some of the spectral smearing observed around regions of contact calls where aperiodic amplitude modulation is also observed (i.e., augmenting the broadband appearance). The overall contribution of each of these mechanisms, aperiodic frequency modulation versus aperiodic amplitude modulation, to the signal spectrum is difficult to estimate when the two processes occur simultaneously, but undoubtedly, both mechanisms contribute to the complex spectra of budgerigar vocalizations. Further acoustical and physiological investigations are needed to elucidate the roles of these mechanisms in the production of budgerigar vocalizations.

6. Additional evidence for the presence of aperiodic amplitude modulation

Insufficient acoustic evidence exists to determine conclusively if all the frequent aperiodic fluctuations in amplitude observed in budgerigar calls arise via amplitude modulation, but, given its demonstrated presence in some portions of calls, and its prominence in English vowel productions, it is distinctly possible if not probable. Further evidence, however, comes from the analysis of contact calls produced by budgerigars with lesions in the vocal control nucleus NLc (central nucleus of the lateral neostriatum). NLc lesions affect the amplitude of the regions of budgerigar calls that fluctuate aperiodically, as well as regions that are clearly amplitude modulated, suggesting that amplitude throughout the entire call is regulated by a common mechanism and is under the control of a neural circuit whose primary target is the syrinx (Banta and Pepperberg, 1997; Banta, 1998). This result would not be expected if the aperiodic modulations of

amplitude observed in budgerigar calls were simply spurious fluctuations as observed in all biological signals.

C. Implications of amplitude modulation for investigations of budgerigar vocalizations

Budgerigars' ability to produce amplitude modulation has significant implications for future investigations of their sound production, and necessitates re-evaluating results and interpretations of previous studies of ontogenetic, neural, syringeal, and acoustic mechanisms underlying their vocalizations. For example, fundamental frequency is an inappropriate concept when considering amplitude-modulated vocalizations. Analyzing a vocalization containing amplitude modulation as if it were harmonic may lead to serious acoustic and physical misrepresentations of the signal. Future investigations of budgerigar vocalizations must include acoustic analyses appropriate for amplitude-modulated signals (e.g., ruling out the possibility that the vocalization is harmonic; ensuring concurrence between the Fourier spectrum and the amplitude waveform), and must use appropriate terminology to refer to vocalization components. Specifically, because the present study raises serious questions as to the nature of budgerigar contact call production and suggests amplitude modulation as the underlying mechanism, use of neutral terms such as ''dominant signal'' may be preferred to terms such as fundamental frequency until the issue is resolved.

The presence of amplitude modulation in vocal signals impacts most significantly researchers' reliance on acoustic analyses performed solely with Fourier techniques. Such analyses may lead to incorrect inferences about the signal source, and the frequencies it produces. Sidebands, for example, which account for most of the components in the Fourier spectrum of a complex amplitude-modulated signal, are not source-produced frequencies, but rather result from nonlinear interactions between two other signals originally produced by the source(s). This inference is not possible solely with visual inspection of the Fourier spectrum. Only after accounting for all frequencies present in the spectrum, and reconciling the amplitude waveform and Fourier spectrum, are the acoustic properties of the source clarified.

1. Mechanical and neural substrates of budgerigar vocalizations

Analyses relying solely on visual inspection of Fourier spectra have led to misinterpretations of the physical, structural, and neural mechanisms underlying production of budgerigar vocalizations. Reports from Heaton *et al.* (1995), Brauth *et al.* (1997), and Shea *et al.* (1997) suggested that budgerigar contact calls are harmonic vocalizations, and that the fundamental frequency of these calls is significantly reduced in birds that have undergone bilateral denervation of the syrinx. Brauth *et al.* (1997) proposed a model for budgerigar syringeal function based on these findings. However, this purported decrease in fundamental frequency has not been reconciled with findings that (a) calls of syringeal denervated birds are essentially a harmonic stack of frequencies (Heaton *et al.*, 1995), and (b) the dominant frequency of these harmonic productions shifts when produced in helium, whereas the dominant frequency of calls of normal, inner-

vated birds does not (Brittan-Powell *et al.*, 1997b). This differential effect of helium would not be predicted if the source frequency was the only feature affected by denervation, but may indicate that the harmonic components of denervated budgerigar calls are produced in a fundamentally different manner than a normal bird's call. Unfortunately, the authors did not report effects of syringeal denervation on the gross temporal envelope or amplitude waveform for any calls they present. Re-evaluation of the results and interpretations from these studies in the context of amplitude modulation might greatly increase our understanding of mechanics of the budgerigar vocal apparatus.

Studies have also fallen unexpectedly short in identifying effects of lesions in the vocal control system on the production of budgerigar vocalizations. To date, few studies have documented the post-lesion fate of budgerigar calls. Hall *et al.* (1994) present data from budgerigars lesioned unilaterally and bilaterally in and around Field L and nucleus basalis (NB). No effects were found following Field L lesions, but NB lesions caused deterioration, loss of individual distinctiveness, and loss of all frequency modulation (as identified by visual inspection of Fourier spectra) of contact calls. What is not known, however, is how lesions affected the gross temporal envelope, amplitude waveform, or amplitude modulation present in these vocalizations. Lack of understanding of the acoustic nature of budgerigar vocalizations may similarly have hindered analyses of other unpublished lesion studies. In contrast, preliminary evidence from recent experiments shows that even small, unilateral lesions in the central nucleus of the lateral neostriatum (NLc) can significantly and specifically affect amplitude modulation found in both budgerigar contact calls and productions of learned English vowel sounds, although the Fourier spectra may appear relatively unaffected (Banta and Pepperberg, 1997; Banta, 1998). Consideration of the acoustic implications of amplitude modulation will facilitate future investigations to define more thoroughly and accurately effects of lesions in vocal control nuclei.

2. Vocal learning

The presence of amplitude modulation in budgerigar vocalizations has intriguing implications for studies of vocal learning. Budgerigars can continue vocal learning throughout adulthood (Brown *et al.*, 1988; Farabaugh *et al.*, 1994), and juveniles require auditory feedback to develop their calls (Dooling *et al.*, 1987). The acoustic or temporal features to which birds actually attend and learn when they begin to produce their first contact calls or modify their adult call repertoire as adults are, however, unknown. Budgerigars' ability to produce a specific pattern of amplitude modulation to mimic English vowels strongly suggests that budgerigars may also ''learn'' when and how to vary amplitude in their contact calls, as well as other conspecific vocalizations. As mentioned previously, a budgerigar call may exhibit 3–5 frequency changes throughout its duration, but 10–15, or more, amplitude changes. Whether all modulations of amplitude are due to the nonlinear process of amplitude modulation (in contrast to simple amplitude fluctuations of the gross temporal envelope, discussed above), is not yet clear but is a dis-

tinct possibility. Perhaps budgerigars learning contact calls learn not only which dominant frequency to produce, and how to vary that frequency, but also a pattern of amplitude modulation. Indeed, perhaps amplitude modulation is *the* critical acoustic feature monitored by budgerigars engaged in vocal learning. Brittan-Powell *et al.* (1997a) and Hall *et al.* (1997) investigated the ontogeny of call production in budgerigars, but not the development of amplitude modulation. Such analyses may greatly improve our understanding of mechanisms underlying vocal learning in this species.

D. Syringeal mechanisms underlying the production of amplitude modulation

Acoustic characteristics of amplitude-modulated vocalizations in songbirds were first described by Nowicki and Capranica (1986a, b). They found that the ''dee'' syllable of the black-capped chickadee (*Parus atricapillus*) call was not a simple harmonic vocalization, but rather resulted from the nonlinear interaction of two harmonic signals. The chickadee, like all songbirds, has two syringeal apertures (one on each side of the tracheobronchial junction), each with a membrane capable of producing a separate sound. Nowicki and Capranica proposed that the spectral characteristics of the ''dee'' arose because each side of the syrinx produced a different frequency. In contrast, the budgerigar, like all parrots, has a single syringeal aperture with two opposing lateral tympaniform membranes (LTMs; Nottebohm, 1976) in the tracheal portion of the tracheobronchial junction, and these membranes purportedly cannot produce sound independently (Nottebohm, 1976; Heaton *et al.*, 1995; Brauth *et al.*, 1997). Thus, how do budgerigars produce amplitude-modulated vocalizations?

A clue about budgerigar syringeal mechanisms may come from research on the monk parakeet, *Myiopsitta monachus*. This bird not only produces amplitude-modulated call-like vocalizations (''a rattling squawk''), but two intrinsic muscles of its syrinx, the syringeus and the tracheobronchialis, are temporally correlated with pulsatile elements of this vocalization (Gaunt and Gaunt, 1985). A similar mechanism may be responsible for budgerigars' production of amplitude-modulated signals. For example, the dominant or carrier frequency may be produced by a flow-induced, self-sustaining oscillation of the LTMs (achieved by Bernoulli action-like forces of air on the LTMs). The carrier frequency amplitude may then be modulated by either adducting or abducting the LTMs (i.e., moving them, respectively, into or out of the tracheal lumen, and thus into and out of the air flow). Although direct syringeal muscle activity may be responsible for producing amplitude modulations of this type in monk parakeet calls (Gaunt and Gaunt, 1985), I find amplitude-modulation rates ranging from 100–742 Hz in the budgerigar. Because these upper frequencies are far greater than the rate at which even the fastest skeletal muscle can contract, direct syringeal muscle activity is not likely responsible for producing the modulating signal in all budgerigar amplitude-modulated vocalizations.

Nonlinear oscillations of the syringeal membranes may also be responsible for producing amplitude modulation in budgerigar vocalizations. Fee *et al.* (1998) describe nonlin-

ear dynamics present in the excised syrinx of the zebra finch (*Taeniopygia guttata*). They postulate that these nonlinear mechanics are responsible for some nonlinear characteristics observed in zebra finch song, such as period doubling, mode-locking, and sudden transitions from periodic to aperiodic or chaotic signals. Tests on a biophysical model of the syrinx further support their hypotheses and suggest that, at least for mode-locking, coupling of the Bernoulli force-driven oscillation to a higher vibrational mode in the membranes may be responsible. Similar mechanisms might produce nonlinear acoustical features of budgerigar vocalizations: Smooth yet rapid transitions in amplitude, and between periodic and aperiodic or chaotic modulations, are evident in regions of calls that lack obvious spectral evidence of amplitude modulation [Fig. 1(B)]. If budgerigars indeed use such mechanisms to mimic the sounds of human speech, they must have central control over at least some aspects of the syringeal dynamics to initiate, terminate, and modulate production of this nonlinear activity. Further experiments are necessary to assess the roles of both the syrinx and the central vocal-control system in producing nonlinear acoustical features of budgerigar vocalizations.

IV. CONCLUSIONS

In summary, evidence presented here supports the conclusion that the nonlinear process of amplitude modulation significantly influences the acoustic properties of budgerigar contact calls and learned English vowel sounds. The mechanisms budgerigars use to produce amplitude modulation are, however, unknown. Future studies considering the presence of amplitude modulation should shed further light on the ontogenetic, physical, and neural bases of budgerigar vocalizations, and, in turn, these studies should further our understanding of how budgerigars produce amplitude-modulated vocalizations.

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